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Breeding and moult cycles were investigated in pairs of European Kestrels *Falco tinnunculus* exposed to four different photoperiods (LD regimes of 17.5:6.5, 15:9, 13:11, and 8:16). Laying, incubation and feeding of the young occurred in all four photoperiods, with all birds moulting after the breeding season. The time until the first egg, the duration of the period during which first clutches were laid, and the time until birds began to moult, were all negatively correlated with daylength.
Two groups of birds (LD 13:11 and 8:16) were held under constant conditions for 4.5 and 2 yr, respectively. After the first breeding/moult cycle, the LD 13:11 group did not begin a second cycle for the next 19 months, and only started laying again, and subsequently moulting, after exposure to an 8 h day for 6 weeks. The LD 8:16 group went through two breeding/moult cycles during the two years.
It is concluded that the development and expression of photorefractoriness is related to daylength, and that photorefractory Kestrels need short days to become photosensitive again. The possibility that the development of photorefractoriness is involved in the seasonal decrease in clutch size, found in both free-living and captive breeding Kestrels, is discussed.

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Introduction

In temperate zone birds, breeding is usually restricted to a small part of the year, generally spring and early summer. This arrangement allows the parents to work for their brood during relatively long days, when environmental conditions are mild and there is increased food availability. It also enables them to finish the moult and prepare for migration later in the year before the days become short and food much scarcer. The reproductive system develops to a very small extent during the short days of autumn after photorefractoriness is ended but development is much greater when the days become longer during late winter and spring. Breeding ends in early summer, when days are still long and this photorefractoriness prevents the birds from continuing to breed into the late summer, thereby delaying processes such as moult and migration until a time too late in the year.

The alternation of a photosensitive and a photorefractory state has been widely documented in birds (Farner et al. 1983, Nicholls et al. 1988) and we briefly mention two of the best studied species. In White-crowned Sparrow *Zonotrichia leucophrys gambelii* (a species that breeds in the east Canadian Arctic tundra during early summer and winters in the southern United States), days of 14 h light or more induce gonadal growth and development, and lead eventuallly to photorefractoriness. In birds exposed to daylengths of between 14 and 20 h the rate of testicular growth increases, and the number of long days required to induce photorefractoriness decreases. Short days are necessary to terminate photorefractoriness. A period of 6 weeks with 6–8 h days is sufficient to induce photosensitivity

Table 1. A summary of photoperiodic experiments indicating the different light regimes, whether they were carried out indoors (I) or outdoors (O), the number of pairs, and their duration (months).

Photoperiod	Location	No. of pairs	Duration
17.5:6.5	I + O	20	9
15:9	I + O	2	10
13:11	I + O	14	9
	I	7	>48
8:16	O	4	34
	I	6	>25

Table 2. A summary of breeding and moult data for the four photoperiodic experiments during the first cycle.

Photoperiod	Mean time until first egg (d)	Laying period of first clutches (d)	Mean time until moult (d)
17.5:6.5	40±11	35	72±11
15:9	55–60	?	9±11
13:11	95±16	51	129±18
8:16 (O)	202±28	69	265±38
8:16 (I)	149±29	65	196±26

(Farner et al. 1983). The European Starling *Sturnus vulgaris* (by origin probably a tropical species, but now breeding in most parts of the world) reacts similarly to long days (Nicholls et al. 1987, 1988). One slight difference, however, is that under short days the reproductive system develops slowly to maturity and then stays in an active state continuously, the birds neither becoming refractory nor moulting. When such birds are exposed to long days the gonads regress after some weeks and a moult takes place. As in White-crowned Sparrows a period of short days is necessary to break photorefractoriness, but uniquely under a LD 12:12 photoregime an alternation of periods of gonadal development and regression/moult can occur in 30% of the individuals (Schleussner 1989). These "circannual" cycles have a period of about 10 months (see Gwinner 1986). White-crowned Sparrows under LD 12:12 develop very irregular testicular cycles with periods much less than one year and of successively smaller amplitude: they show no signs of photorefractoriness (Farner et al. 1983).

Photorefractoriness is a photoperiodically driven phenomenon developing within the central nervous system. This has been most clearly demonstrated in the Starling where the Gn-RH neurosecretory system undergoes major changes in both morphology and content as refractoriness develops, and as it dissipates (e.g. Foster et al. 1987, Goldsmith et al. 1989, Dawson and Goldsmith 1989).

No experiments have directly addressed the photoperiodic response systems in raptors, although Bird et al. (1980) did manage to breed American Kestrels *Falco sparverius* during the winter. The European Kestrel *Falco tinnunculus* is a single-brooded raptor with a population laying period of about 70 days, from early April until early June, followed by a 4–5 month moult period. It has been studied extensively in the Netherlands (Cavé 1968, Masman 1986, Daan et al. 1988, Dijkstra 1988, Meijer 1988). This paper reports on breeding experiments with this raptor exposed to short and long photoperiods and it addresses the question of the development of photorefractoriness, and discusses the possibility that the development of photorefractoriness is involved in the seasonal decrease in clutch size found in this and many other single-brooded birds.

Methods

Experiments over the period 1984–1988 used 53 pairs of Kestrels breeding in four different photoperiods (8, 13, 15 and 17.5 h of light). Birds were housed in 2 × 1.5 × 2 m light-tight indoor or outdoor cages, each with a fluorescent lamp providing 200 lux light intensity in the middle of the cages. In the outdoor cages temperature was not controlled, but indoors it was held at 17 ± 2°C (Meijer 1989).

Food (dead laboratory mice and chickens) was provided ad libitum every day at 15.00 hours. In two photoperiods (LD 13:11 and 17.5:6.5) some pairs were food restricted for a short period to delay laying until the second half of the breeding season (see Meijer 1989 for details). Normally, the photoperiodic experiments ran from December until the next September/October, but two lasted for several years (see Table 1). The birds in the LD 13:11 schedule were exposed twice to an episode of short days (LD 8:16), the first time after 27 months (for 6 weeks), and the second time after 42.5 months (for 10 weeks). The weight of the birds and their moult were checked regularly (every 2–4 weeks).

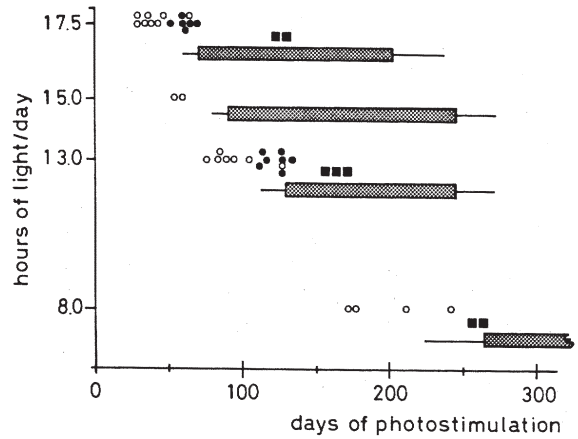

Fig. 1. Timing of laying (circles and squares) and moult periods (hatched bars, mean onset and end ±sd) of pairs of Kestrels exposed to LD 17.5:6.5, 15:9, 13:11, or 8:16. First clutches of pairs with (○) ad libitum food and (●) of pairs food restricted for a brief period at the start of the experiment. ■ second clutches.

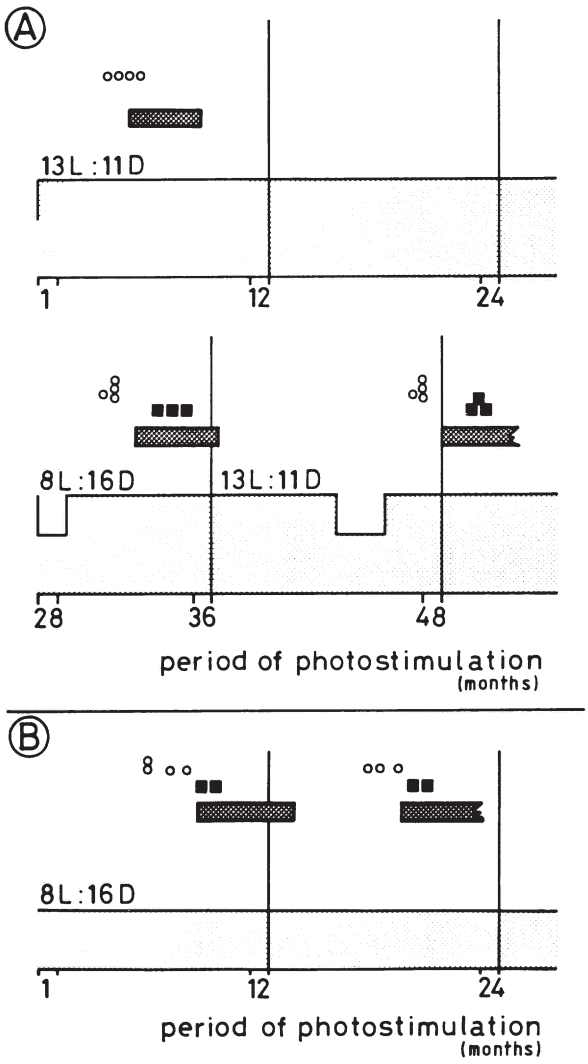

Fig. 2. Laying (circles and squares) and moult periods (hatched bars) of two groups of Kestrels held under constant photoperiods for 4.5 (2A) or 2 (2B) years, respectively. The pairs in the 13-h day (2A) were twice exposed to a short day of 8 h (after 27.5 months for 6 weeks and after 42.5 months for 10 weeks, respectively).

Results

Laying occurred in all four photoperiods, and in every case 60–70% of the pairs laid eggs, incubated and successfully reared their young. As Table 2 and Fig. 1 show, however, the time until eggs were laid, was inversely related to photoperiod-length. The extremes occurred under LD 17.5:6.5 when the first egg appeared after 28 days (mean: 40 days) and LD 8:16 (indoor) when the first egg was laid only after 173 days (mean: 202 days). A correlation analysis confirmed the negative relationship ($y = 336$ days $- 18L$, $n = 4$, $r = 0.98$, $p < 0.01$, Table 2).

Also, the duration of the first laying period (the time interval between breeding attempts of the first and the last pair in each group) was negatively correlated with daylength (see Table 2: $y = 98$ days $- 3.6$ L, $n = 3$, $r = 0.99$, Table 2). In three of the four photoperiods (Fig. 1) some females laid second clutches, at around the time when the young of the first brood left the nestbox. The interval between first and second clutches ranged from 90–102 days and was not related to daylength (Fig. 1).

After the breeding season all birds moulted. Mean moult onset was again negatively correlated with daylength ($y = 367$ days $- 17.5$L, $n = 4$, $r = 0.99$, $p < 0.01$, Table 2) with the birds in the 17.5 h day beginning their moult after 72 days (± 11, $n = 40$), whilst in the 8 h day (indoor) it only began after 265 days (± 38, $n = 12$). Data on moult duration are confounded by differences between the sexes, between breeders and non-breeders, and between breeders laying one or two clutches (see Meijer 1989) but, overall, birds in the 13 h day moulted faster (120 ± 20 days, $n = 29$) than birds in all other groups (Fig. 1).

Two groups of birds (LD 8:16 and LD 13:11) were retained in the constant LD conditions for more than one breeding/moult cycle. Three of the four pairs in the short photoperiod (LD 8:16, outdoor) laid during the first cycle and also during the second and third cycles, with all birds ($n = 8$) starting to moult after each of the three breeding periods. This experiment was repeated indoors (Fig. 2B). Four of the six pairs started laying after 202 ± 28 days, and all birds ($n = 12$) started to moult after the breeding season. After 549 (± 18) days three pairs laid again and all birds subsequently started to moult. None of the birds in the relatively long photoperiod (LD 13:11) laid or moulted a second time during the experimental period of 27 months. Two new breeding/moult cycles could have occurred in such a period (Fig. 2A). After exposing the seven pairs to LD 8:16 for 6 weeks, four pairs laid within 69–76 days, and all birds ($n = 14$) started to moult on average 106 (± 31) days after the photoperiod returned to 13 h. After 42.5 months (i.e. after 14 months on a 13-h day, a period in which another breeding/moult cycle was possible), the four pairs which had laid during the first two "breeding seasons" were again exposed to a 8 h day (for 10 weeks). Upon return to LD 13:11, all four pairs began to lay (51 ± 5 d) and subsequently moulted (Fig. 2A).

Discussion

Most photoperiodic experiments in birds have measured reactions of the hypothalamo-pituitary-gonadal axis in different daylengths, and have usually focused upon the reactions of the males, since female passerines lay only rarely in captivity. This, therefore is a rare experiment since it investigated under semi-natural conditions in four different photoperiods the normal reproductive behaviour, including incubation and feeding of

the young. The results show that the length of the day was inversely correlated with the time to onset of laying, and with the period during which first clutches were started. These findings are in general accord with the reactions of the male of other species (see Nicholls et al. 1988), in which longer days induce faster development and earlier regression of the reproductive system. In contrast to the migratory White-crowned Sparrow, in which the reproductive system develops only in days of 14 h or more (and therefore not on the wintering grounds), Kestrels develop the reproductive system also under short days. This phenomenon also occurs in European Starlings. The recrudescence of the Kestrel's reproductive system during short days (normally in autumn) is supported by three observations on birds under natural photoperiodic conditions. Cavé (1968) showed that in (resident) female Kestrels caught in the middle of Holland during autumn (when daylength decreases from 12 to 8 h) the ovaries developed slowly. Secondly, territorial interactions between males are concentrated during early spring, but there is a second peak in autumn, when also the first juveniles males try to occupy new territories (Masman 1986). Finally, at the endocrine level there are indications that the reproductive system of Kestrels is reactivated during autumn. Luteinizing hormone (LH) concentrations in free-living and captive birds, sampled in September-November were above the levels found during the refractory period, although androgen concentrations were still minimal (Meijer, unpublished data). Theorectically then, it should be possible for a Kestrel to breed in autumn, as reported in some mild years for Starlings and ducks in England (e.g. Snow 1955), but at least two factors normally make this impossible. Firstly, the development of the reproductive system would take too much time under these short days: eggs would be expected after 336 – 18 × 10 = 156 days under a 10-h day (see Fig. 1). Assuming moult finishes in early October (Meijer 1989) and the birds become photosensitive soon thereafter, then laying would only start in early March. Secondly, in the short winter days it is impossible for the male to collect enough food for himself, the laying and incubating female and, later on, the young (Masman 1986).

The development of photorefractoriness in the Kestrel is negatively correlated with daylength, assuming that full photorefractoriness coincides with the end of the breeding season and with the start of moult (see Nicholls et al. 1988). In contrast to Starlings, in which photorefractoriness occurs only in days of 12 h or more, Kestrels also seem to become photorefractory on LD 8:16. The photorefractoriness prevents free-living Kestrels from continuing to breed in June and July, when conditions, most notably increasing numbers of *Microtus* voles would allow them to lay a second clutch. There must be other long term constraints on laying a second clutch, which have retained such a rigid form of refractoriness in the Kestrel.

The birds in the 13-h day, which did not breed again for a period of 19 months, show clearly that this photoperiod is too long to break the photorefractory state. Like virtually all other birds, Kestrels need short days to become photosensitive again. Pairs of Kestrels in the 8-h days (in outdoor as well as in indoor aviaries) showed an alternation of breeding/moult cycles. This short day seems long enough to develop the reproductive system in photosensitive birds (although it takes a relatively long time), and is short enough to break photorefractoriness later on.

Under constant daylenghts laying was clearly divided into two phases (see Figs 1 and 2), two-thirds of the pairs laying one clutch, and one third managing a second clutch. Second clutches (i.e. laying after successfully fledging the young of the first brood) were found neither in free-living birds during 1977–1990, nor in our captive breeding colony under natural days during 1983–1990.

The steady development of photorefractoriness as the season progresses could itself be reponsible for the seasonal decrease in clutch size of the Kestrel (this decrease seems to be internally programmed, see Meijer 1989). In this context it is important to realise that whilst the *expression* of refractoriness – gonadal collapse, onset of moult – occurs suddenly, the development of the underlying phenomenon has been progressive over many weeks before its actual expression (see Fig. 2 in Follett and Nicholls 1984 for a model and also Nicholls et al. 1988). There are a number of observations which favour this idea of a seasonal decrease in clutch size being caused by a slow progressive switching off of the female reproductive system. Firstly, plasma LH levels of (male and) female Kestrels held on 17.5 and 13 h photoperiods initially increase sharply but then decrease spontaneously, the rate of decrease being positively correlated with the length of the photoperiod (Meijer 1989). Secondly, in both American and European Kestrels the capacity to lay new eggs after egg removal decreases with time during the breeding season. Continuous egg removal in the American Kestrel causes, at the onset of the breeding season, females to lay 20–30 eggs, whereas at the end of the season they only respond by laying 4–5 eggs (Porter 1975). Also European Kestrels seemingly react to egg removal only early in the season (Beukeboom et al. 1988). Thirdly, there is a slow but spontaneous increase in incubation behaviour during the breeding season, causing later laying females with smaller clutches to spend more time incubating their first laid eggs. This is now documented for Great Tits *Parus major* (Haftorn 1981, 1985), Kestrels (Beukeboom et al. 1988) and Starlings (Meijer 1990), and may be related to the development of photorefractoriness. Developing this idea further it is tempting to suggest that the progressively smaller clutch size is a direct reflection of prolactin secretion. In birds, as in mammals, prolactin is secreted at higher levels under long days (e.g. male Starling: Dawson and Goldsmith 1983, Goldsmith and Nicholls 1984, Dawson et al.

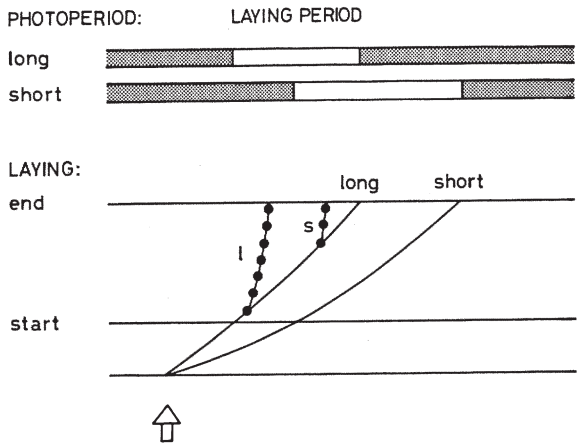

Fig. 3. Schematic representation of the development of photorefractoriness in a long and short photoperiod, and the occurrence and length of the two corresponding laying periods. In the long photoperiod an early and a late female is shown, laying a large (l) and small (s) clutch, respectively. Start of the photoperiodic experiments with photosensitive birds is indicated with an arrow.

1988), this long-day effect being separated from the extra incubation-induced rise occurring as the eggs are incubated. Two possibilities exist: (1) the rising prolactin level during the breeding season potentially suppresses gonadotrophin secretion and hence truncates the number of ovulations and/or (2) the higher background prolactin means that when eggs are laid the incubation-induced rise reaches the ovulation-suppression level earlier and so the bird ends egg-laying prematurely. Evidence for these ideas is still fragmentary, but we showed earlier (Meijer et al. 1990) that in captive female Kestrels, prolactin concentrations significantly increase during spring, however have the same level in early and late laying females.

A final point concerns the rate at which refractoriness develops. It should develop faster in the long photoperiods (resulting, in our breeding pairs, in an early and short laying period), and more slowly in the short photoperiods (resulting in a later and longer laying period, see Fig. 3). The data support this with later and longer laying periods in shorter photoperiods, compared with those in longer photoperiods (see Fig. 1). If the rate of clutch size decrease is coupled to the rate at which photorefractoriness develops, then we would predict a slower decrease in clutch size in shorter photoperiods. Clutch size decreases in the 17.5 and 13 h photoperiods at the rate of 0.046 egg d^{-1} (Meijer 1989), in the 8-h photoperiod (outdoor) we found no decrease at all in three successive cycles (Meijer, unpubl. data). All these findings (changes in LH levels, decreasing capacity of the ovary to develop eggs, increasing prolactin levels, the occurrence and length of the laying periods) support the view that the development of photorefractoriness, or a slow spontaneous turning off of the reproductive system could be responsible for the seasonal decrease in clutch size, found in so many single-brooded species. Direct experimental tests are now needed to test this hypothesis.

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